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CHRONOLOGICAL SURVEY OF THE TETRAPOD-BEARING TRIASSIC OF ARGENTINA

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SUMMARY OF PREVIOUS WORK

Ever since 1958, Argentinian paleontologists have been working intensively on continental Triassic outcrops bearing tetrapod remains, inspired by A. S. Romer's successful expedition to Mendoza and San Juan provinces in that year. The resultant collections are from both new and previously known localities; they come mainly from the Ischigualasto Formation, worked on by Romer, but also include material from a number of other formations. Exploring and collecting trips to La Rioja, San Juan, San Luis, Mendoza, and Santa Cruz provinces were made possible by many grants from the Consejo Nacional de Investigaciones Científicas y Técnicas. This support has enabled us not only to make good collections from previously known fossil-bearing localities, but also to discover new fossiliferous areas, which have broadened our view of Argentinian Triassic faunas. Materials collected in recent years include fossils from three localities in the Ischigualasto Formation, from the Los Colorados Formation of La Rioja and San Juan provinces, from the Cacheuta Formation in northern Mendoza Province, and, in addition, from a new locality in the Puesto Viejo Formation south of San Rafael, Mendoza Province, discovered by the former Dirección Nacional de Geología y Minería. A great proportion of the tetrapod material collected has been studied, and it is possible to identify the remaining material with satisfactory approximation: these studies enable us to attempt an interpretation of the chronology of some of the Argentinian Triassic formations.

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The chronology of these Triassic series has, in the past, been interpreted largely on the basis of their paleobotany, which was well summarized by Bonetti (1963). These interpretations, unfortunately, are not in complete agreement with those obtained from a study of tetrapod remains; the paleobotanic data indicate little differentiation from one formation to another, while the tetrapod data suggest clear differences, and allow a better analysis of chronology.

Bonetti's work is the most recent on the subject. She accepts the opinion of Groeber and Stipanicic, 1953, and Stipanicic, 1957, that the known Argentinian Triassic series with Dicroidium flora are (when present) in discordance over rocks synchronic with those known as Choivoiliteuse from southern Mendoza and northern Neuquén provinces. The correlation proposed by these authors, between the Argentinian Choivoilitense and the Porfidicqueratofiric series of the Chilean coast south of Los Vilos, is also accepted by Bonetti. She concludes that the Argentinian Triassic series with Dicroidium flora are essentially of Keuper age (Carnian at the lower levels, Norian at the upper). This conclusion is based on the presence of an ammonite and pelecypod fauna in sediments underlying the effusive rocks near Los Vilos, as well as on the affinities of a flora found in a lutitic level intercalated in the upper part of the Chilean effusive complex with the Argentinian Triassic flora from the Potrerillos, Cacheuta, Barreal, Cortaderita, etc., formations. In her clear and brief analysis, however. Bonetti points out the need for re-examination of the determinations of most of the marine fauna below the Los Vilos effusives. Quite apparently, the chronology of the Chilean effusive series is far from definitely clear.

In recent years some attempts at Triassic chronology have been based on tetrapod remains. Owing to the presence of Chirotherium footprints studied by Rusconi (1951b) and reconsidered by Peabody (1955), Stipanicic (1957) considered that the Sierra de las Higueras Formation in northern Mendoza was the oldest Triassic formation of Argentina, and referred it to the Neoscythian — Eoanisian. Romer (1960, 1962b) believes that the age of the Ischigualasto Formation is upper Middle Triassic: "surely pre-Norian and not improbably pre-Carnian." Reig (1961) considered briefly the age of four Triassic formations. He believes that the Cacheuta Formation, with both brachyopids and a proterosuchian, is more reasonably assigned to the "Eotriásico Superior" (Scythian) than to any later time. As to the age of the Sierra de las Higueras Formation as given by Stipanicic,

Reig points out the limited significance of the footprint data. As regards the Los Rastros and Ischigualasto formations, after some analysis and comparisons, he assigns an upper Ladinian age to the Ischigualasto fauna.

	Stipanicic 1957	Bonetti 1963	Reig 1961 , 1963	Romer 1960,1962
NORIAN	Los Colorados Ischigualasto	Los Colorados		
	Los Rastros	Ischigualasto		
CARNIAN	Ischichuca	Los Rastros		
		Ischichuca		
LADINIAN			Ischigualasto	Ischigualasto

Table 1. Recent chronological interpretations of some Triassic formations of Argentina.

ANALYSIS OF VERTEBRATE FAUNAS

Puesto Viejo Formation (Mendoza Province). — The fauna of these red sandstones comprises, so far as is now known, only therapsids of the infraorders Cynodontia and Dicynodontia. The cynodont Pascualgnathus polanskii Bonaparte (in press.b), known from very complete remains, is a diademodontid. It has affinities of great significance with Trirachodon, and of lesser significance with Diademodon. Among these points of similarity are important characters of the skull and jaws, the tooth row, the secondary palate, and so forth; in the axial region of the postcranial skeleton we also find good characters for the family assignation. Pascualgnathus is closer to African genera than to other cynodonts from South America or from other continents; it represents, therefore, an assemblage different from that common in South America, and provides new evidence of some type of vinculum between Africa and South America not detected in the case of other tetrapods from the South American Triassic.

Recent work on *Diademodon rhodesiensis* Brink (1963) and on a *Trirachodon*-like genus (Brink, 1963; Kitching, 1963) demonstrates that these genera survived beyond the end of the

Lower Triassic. They have been found in the Ntawere Formation, which immediately follows the *Cynognathus* Zone and is thus of probable Anisian age. As *Pascualgnathus* is but little advanced anatomically beyond *Trirachodon* and *Diademodon*, I have considered this genus to be also Anisian (Bonaparte, in press.b.c).

The dicynodont of this formation has been referred to the African genus Kannemeyeria, as K. argentinensis Bonaparte (in press,b), because of the great similarity between its skull and that of Kannemeyeria sp. (Watson, 1948, fig. 17) from the Cynognathus Zone. (Kannemeyeria argentinensis is a smaller species than the African representatives of the genus, so that posteranial similarities are less noticeable.) There are clear generic differences between K. argentinensis and other kannemeyerid genera. Until recent years, Kannemeyeria was unknown outside of the Cynognathus Zone, but a form referable to Kannemeyeria is cited by Kitching (1963) from the Ntawere Formation, and a Kannemeyeria from the Manda Formation of the Ruhuhu Valley in Tanganyika is reported by Cox (1965) and Brink (1963). It is thus apparent that Kannemeyeria survived into the Anisian; we can, consequently, consider K, argentinensis to be either Scythian or Anisian in age. The presence of Pascualgnathus, however, leads us to consider the therapsids of the Puesto Viejo Formation as Anisian.

Potrerillos Formation (Mendoza Province). — Fragmentary remains of a cynodont jaw constitute the only available tetrapod material from this formation. Minoprio (1954) studied these remains, and erected a new genus, Colbertosaurus, which he placed in the Ictidosauria. However, the principal anatomical feature used by Minoprio in his identification of Colbertosaurus as an ictidosaurian — the placement of the posterior part of the tooth row — is a common feature among the gomphodont evnodonts from the African Middle Triassic and the South American Middle or Upper Triassic: Colbertosaurus is thus more reasonably considered a gomphodont cynodont than an ictidosaurian (see Bonaparte, 1962). Colbertosaurus can best be compared with Pascualanathus, from the Puesto Viejo Formation. The two have many features in common: the type of postcanine implantation, the number and size of the incisors, the large section of canines, the larger size of the postcanines in the middle of the tooth row, and the type of jaw constriction behind the canines. Pascualgnathus has eleven postcanines and Colbertosaurus nine.

It is evident that there is a significant, although limited, resemblance between the two genera. The Potrerillos Formation may therefore be considered, at least on the basis of present knowledge, as very close in age to the Anisian Puesto Viejo.

Cacheuta Formation (Mendoza Province). — From this formation we know two brachyopid labyrinthodonts, apparently representing two separate genera — Pelorocephalus Cabrera (1944) and Chigutisaurus Rusconi (1948). We also have the posteranial skeleton of a proterosuchian, Cuyosuchus Reig (1961), which was described by Rusconi in 1951 as a brachyopid.

Watson (1956) agreed that *Pelorocephalus* is a brachyopid, and accepted as valid the affinities claimed by Cabrera between *Pelorocephalus* and *Batrachosuchus* from the *Cynognathus* Zone. As Watson pointed out, brachyopid labyrinthodonts are known only from the Permian and Lower Triassic throughout the world.

These labyrinthodonts from the Cachenta Formation require further study; it is possible that in the palatine features of the two genera there are similarities with Batrachosuchus, but the difference in skull height in Chigutisaurus, as well as its larger size, may indicate that the Argentinian brachyopids, perhaps because of peculiar ecological conditions, outlasted the Scythian. It would, of course, be out of the question to call them Keuper: tentatively we may consider them to be of Anisian age. Cuyosuchus, as mentioned above, is considered by Reig (1961) to be a proterosuchian; Hughes (1963) and Tatarinov (1961) agree with this designation. At present, all the more or less well known proterosuchians are of Scythian age, so that there is chronological agreement between them and the brachyopids. Thus, taking into consideration the possible special ecological conditions mentioned above, as well as some features of the Chiqutisaurus skull, the fauna of the Cacheuta Formation is probably Anisian.

Sierra de las Higueras Formation (Mendoza Province). — The only fossil remains from this formation are a group of footprints representing five or six different forms, most of them observed and collected in 1963. Rusconi (1951b) studied a Chirotherium footprint showing an incomplete track of a hind limb and a probable track of the forelimb. Rusconi called them C. higuerensis: Peabody, in 1955, restudied these footprints, and assigned them to C. barthi from the Moenkopi Formation of the United

States. Reig (1961) and Casamiquela (1964) have demonstrated the weakness of such identifications, particularly as they are based on footprints which are far from clear. As mentioned above, Stipanicic (1957) considered the Sierra de las Higueras Formation to be Neoscythian-Eoanisian.

Among the footprints collected and observed in 1963 near Puesto de las Higueras, there is one similar to that of Rigalites Huene (1931) from the Los Rastros Formation. The others are referable to a lacertiform and to therapsids. It seems useful to examine the chronological position of C. hiquerensis and the Rigalites-like genus together, rather than to examine C. higuerensis alone. A first point is that the structure of the foot of Actosauroides from the Ischigualasto Formation, which is known more or less in detail, is in agreement with the footprint of C. higuerensis. A second is that the footprints assigned to Rigalites from Las Higueras are probably not older than the Rigalites from the Los Rastros Formation. My interpretation is, of course, open to question, but it appears highly unlikely that the upper section of the Sierra de las Higueras Formation would be older than the Los Rastros. In consequence, I assume a Ladinian age for this formation.

Los Rastros Formation (San Juan Province). — The only known remains from this formation are good footprints of an archosaurian, Rigalites ischigualastianus Huene (1931). Huene considered them to be footprints of an ornithischian, but this is far from well established. Reig (1961), on the other hand, after study of the limbs assigned to Saurosuchus from the Ischigualasto Formation, believes that these footprints may well have been made by a pseudosuchian of great size, comparable to Saurosuchus. This idea appears to be more acceptable. Despite the fact that these footprints are very clear, their age is not easy to ascertain. Some inferences may be made from the fact that the Los Rastros Formation is overlain concordantly by the Ischigualasto Formation, the age of which is fairly well defined. On this basis, we conclude that the Los Rastros would not be younger than Upper Ladinian.

Ischigualasto Formation (San Juan and La Rioja provinces). — Cabrera (1944) first studied remains from the Ischigualasto Formation, which had been collected by Frenguelli. In recent years, a goodly number of papers on this fauna have been published, greatly increasing our knowledge of this, the richest Triassic tetrapod fauna of Argentina. These include papers by Reig (1959, 1961, 1963), Casamiquela (1960, 1962), Cox (1962,

1965), Romer (1962a), and Bonaparte (1962, 1963a-e, in press.a, b). The fauna of the Ischigualasto Formation is composed of six different groups; these will be discussed individually.

- (1) Labyrinthodontia. Promastodonsaurus bellmanni Bonaparte (1963a) is represented by incomplete remains of the skull, jaws, and pectoral girdle. It has been assigned to the Capitosauridae, and closely resembles Mastodonsaurus from the Lower and Upper Triassic of Europe. As an indication of the chronology of the formation, it is, thus, of little value.
- (2) Cynodontia. The cynodonts are very numerous in this formation, and are found in nearly all its levels. The carnivorous cynodonts are represented by a few specimens referred to Chiniquodon from the Santa María Formation of Brasil (Bonaparte, in press.a). The gomphodont evnodonts are Exacretodon Cabrera (1944), Proexaeretodon Bonaparte (1963d), and Ischignathus Bonaparte (1963c); all three genera are found at approximately the same levels. Exacretodon and the apparently somewhat less specialized Prograeretodon are comparable with the Brasilian Traversodon and with Scalenodontoides from the Middle Triassic sensu lato of Africa (Crompton and Ellenberger, 1957). Ischignathus shows clear advances over the Brasilian and African Middle Triassic cynodonts, particularly in its palatine structure, which resembles that of the tritylodonts. Present knowledge indicates that the cynodonts from Ischigualasto are a little younger than those from Brasil; they are obviously older than the tritylodonts from the redbeds of Africa.
- (3) Dieynodontia. The only known genus of this group is *Ischigualastia* (Cox, 1962, 1965). Cox believes that *Ischigualastia* gives us no decisive chronological data, as it could be considered either Ladinian or Carnian.
- (4) Pseudosuchia. The genera of Pseudosuchia from this formation are Saurosuchus and Proterochampsa (Reig. 1959, 1961) and Aetosauroides and Argentinosuchus (Casamiquela, 1960, 1962). Reig considers that the rauisuchid ornithosuchian Saurosuchus is not only the largest genus of this family, but has a longer ischium and ilium, and a weaker femur than do Prestosuchus from Brasil or Stagonosuchus from Africa. We can assume that these characters represent anatomical advances over the Brasilian and African rauisuchids, comparable to the position noted in the cynodonts. Proterochampsa is considered by Reig as a true crocodilian. New materials of this genus, however, indicate the need for a reconsideration of its position, particularly because of the primitive palatine structure. Actosauroides, well analyzed by Casamiquela (1962), shows important

similarities to Actosaurus (from the German Keuper) in characters of the skull, vertebral column, pelvic and pectoral girdles, limbs, and armor. Some differences may be noted in the teeth, which indicate that Actosauroides may be slightly more primitive than Actosaurus (Casamiquela, pers. com.). Actosaurus and the related genus Stagonolepis (fide Walker, 1961) are from the European Norian. In consequence, it is clear that Actosauroides, if not actually Norian, cannot be too far from this age. Argentinosuchus is known only from a humerus, some fragments of the radius and ulna, and some dermal scutes, and is, tentatively assigned to the Stagonolepidae. As the principal diagnostic parts of this genus are missing, however, its chronology is dubious.

(5) Saurischia. Three genera of saurischian dinosaurs are known (Reig, 1963); a carnosaurian, Herrerasaurus; a coelurosaurian, Triassolestes; and Ischisaurus, of uncertain affinities. Herrerasaurus, known from good material of the posteranial skeleton, and from fragments of jaws which have been referred to it, is considered by Reig as more advanced, in some features at least, than other Triassic carnosaurians. Triassolestes is based on an incomplete skull and jaws, and some posteranial material. Reig reports some affinities with Coelophysis from the Upper Triassic, the only genus included in his comparison, and considers as possible the inclusion of Triassolestes in the Podokesauridae. The affinities of Ischisaurus, which is based on some posteranial remains and fragments of the skull and jaws, are uncertain; there are possible resemblances in the limb bones to Triassic pachypodosaurians.

Little can be inferred regarding chronological position from these incompletely known saurischians. Since all of the comparisons have been made with Upper Triassic forms, we have no valid arguments at present to consider them older than the Keuper; we may, then, assign them to the Carnian.

(6) Rhynchosauridae. Complete remains of these curious forms have been found at different levels of the Ischigualasto Formation. Until the present, unfortunately, no study has been made of them. Some general features of the skull and jaws of these rhynchosaurs resemble those of *Cephalonia* (or *Scaphonyx*) from Brasil. No chronological data can be drawn from these unstudied forms.

In several genera of the fauna of the Ischigualasto Formation, then, we find some advances over related Brasilian genera. It is also evident that the aetosaurid *Aetosauroides*, the traversodontid *Ischignathus*, and the three saurischians appear as forms

more related to Upper than to Middle Triassic faunas. On the other hand, the numerous cynodonts indicate a Middle Triassic age for this formation; their abundance, however, could be explained by supposing that ecological conditions permitted a later expansion of these forms. The advanced features of the cynodont Ischianathus, which has departed far from the known structure of the African Middle Triassic eynodonts, would support this view. The presence of both rhynchosaurs and cynodonts has been considered by Romer (1960, 1962b) as strong evidence that this is an upper Middle Triassic fauna — as noted above, "surely pre-Norian and not improbably pre-Carnian." But the fact that rhynchosaurs from the Norian or Carnian of India have been found associated with a phytosaur, with a form comparable to a coelurosaurian, and with prosauropod fragments (Jain, Robinson, and Chowdhury, 1964), makes his hypothesis of limited validity. In addition, rhynchosaurs have been reported from England, found in association with the supposedly Norian Stagonolepis. In consequence, we may consider the fauna of the Ischigualasto Formation as of Carnian age.

Los Colorados Formation (San Juan and La Rioja provinces). — In the past three years, much good tetrapod material has been found in this redbeds formation. This material is presently under study, but some general considerations are possible at this time. The Los Colorados Formation lies concordantly over the Ischigualasto Formation, and is about 800 m thick. At its base has been found a skull and jaws comparable to Ischigualastia, indicating the possibility of the survival of some genera common to the Ischigualasto Formation. But from the middle and upper sections of the Los Colorados we have found a completely different assemblage of tetrapods. At least three or four genera of prosauropods, some of great size, have been found. In addition, almost complete remains have been discovered of an aetosaurid closely related to Actosauroides, but with more highly specialized teeth and cranial features; apparently this is a Norian fauna.

Our attempts to interpret the chronology of these Argentinian Triassic formations have been based on the currently accepted diagnoses of the Upper Beaufort and Stormberg Series of Africa, the Upper Scythian for the Cynognathus Zone, and so on. These attempts have been based solely on tetrapod remains from which excellent data have been obtained, particularly from the numerous forms comprising the fauna of the Ischigualasto Formation and from the two genera of the Puesto Viejo, which are

so closely comparable to African genera. This work raises the question of the age generally accepted for the Choiyoilitense and its correlations. Apparently this effusive series must be placed in the lower Middle Triassic, or else its correlations with Famatinense and Paganzo III are in need of re-examination.

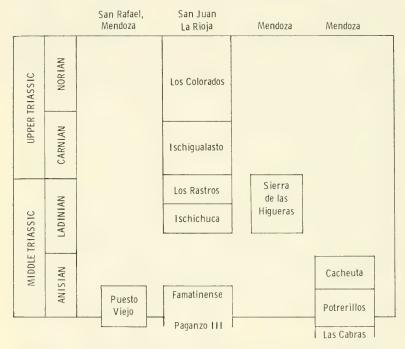


Table 2. A new attempt at chronology of some Triassic formations in Argentina.

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